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FOREST INSECT INVESTIGATIONS

REGIONAL SURVEY STUDIES

No. 1

THE COMPOSITION OF FOREST INSECT INFESTATIONS IN PONDEROSA PINE AS
DETERMINED BY STEM ANALYSES

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FOREWORD

In 1931 The Regional Survey was initiated with two objectives in mind. The first of these was to secure pertinent records to be used as a basis for furnishing information on infestations and trends. This objective has been reported on currently in the various yearly reports on forest insect conditions in the forested areas covered by the Survey.

It soon became apparent that a satisfactory basis for estimating losses was lacking. Any estimates, resulting from the use of estimating methods already developed, were inaccurate. Accordingly, it was determined to make a study of the basis of variation in loss and, if possible, secure a formula that could be applied in estimating under California conditions. This phase, for the present, has been completed and reported on by F. C. Johnson, under the title "Correction Factors for Use in Estimating Total Seasonal Barkbeetle Losses in California." This paper was the first investigative report presented in connection with the Regional Survey.

The second objective of the Regional Survey is to study the factors responsible for infestations, variations in them, and trends exhibited by them. This is an extremely broad field. A preliminary scanning of the information that has been gathered to date concerning various phases of the second objective has been made. It has been found some phases not now being covered should be planned for. In some portions of the complete project a short period of record will be sufficient to secure the necessary data. In others a ten year record will but give a start to the work. In other words, the field is so broad and the variation in requirements for completion of the different phases of the project so varied, that it seems impossible to attempt a general summation of all phases in one report or at stated intervals. In addition, as the work progresses, there is a need for accumulation of data so that necessary and closely correlated laboratory projects can be planned and executed when needed.

Accordingly, it is planned to divide the field of work into less inclusive problems and present the results in informal and preliminary reports. Where possible these reports will present conclusions, but for the most part it is expected they will serve as a means of finding out what has been done and what it seems advisable to do, as well as give information as to the direction the work is taking. Inasmuch as a complete periodical survey of all the work would take too much time and, with press of other projects probably could not be completed in a satisfactory manner, it is believed that this manner of handling the work will prove to be the better method.

REGIONAL SURVEY STUDY NO. 1.

THE COMPOSITION OF FOREST INSECT INFESTATIONS IN PONDEROSA PINE AS DETERMINED BY STEM ANALYSES

INTRODUCTION

The western pine beetle (Dendroctonus brevicornis Lec.) always has been considered the most destructive and important insect attacking ponderosa pine (Pinus ponderosa Lawson). However, it has long been recognized that the entire infestation in any given area or even in individual trees is not always due to that species of insect alone. Infestations by the mountain pine beetle (D. monticolae Hopk.), turpentine beetle (D. valens Lec.), flat-head borers (chiefly Melanophila californica VanDyke), and the pine engraver beetles (Ips emarginatus (Lec.), I. confusus (Lec.), and I. oregoni (Eich.)) often have been of importance.

Other than information resulting from general observation or basal examinations of infested trees few definite indications of the relative importance of the several species of insects have been secured. This has been due to the difficulties of securing stem analyses of infested trees without heavy investments in labor. However, recent control projects in California furnished the opportunity for securing a large number of stem analyses which have been analyzed with the following objectives in mind.

1. What is the relative importance of the several species of insects concerned in infestations due to (a) habits of attack and (b) amount of infestation?
2. What are the common and important infestation types?
3. Is actual composition of infestation indicated by basal sampling methods?
4. What appears to be the significance of variations in composition from year to year or as between different areas?

MATERIALS AND METHODS

Through the cooperation of Forest Service officers and members of the Bureau of Entomology and Plant Quarantine staff at Berkeley, 782 stem analyses of infested trees were secured during the period of 1931-1934. These samples came from 11 different areas. In some cases random sampling methods were used. In others the entire infestation on a given area was analyzed. In all cases it is considered a representative sample was secured. Table 1 gives the pertinent information concerning the samples.

TABLE I

National Forest	Type	Environment	Plot	Acreage	Year	Trees Analyzed	No. Sq. Ft. Bark in Sample
Sierra	WestSide PI	RS. 7	320	1931	124	56,117	
"	"	"	"	1932	49	16,627	
"	"	"	"	1933	56	23,523	
"	"	JP	8	1931	19	11,245	
"	"	SP-JP	9	1931	10	7,679	
"	"	PP	10	80	1933	8	3,347
"	"	SP-PP	12	320	1932	31	24,028
"	"	"	12	"	1933	18	11,042
Stanislaus	"	"	14	"	1932	18	9,046
"	"	"	14	"	1933	12	6,493
Modoc	EastSide PP	Random Sample	1931	130	60,453		
"	"	"	1932	41	19,308		
"	"	"	1933	51	21,281		
"	"	FRS 11	320	1932	54	24,155	
Lassen	"	Las. 6	"	1933	14	4,863	
"	"	"	3	1934	57	25,615	
"	"	"	2	1934	90	36,348	

Totals, West Side type areas	345	169,137
Totals, East Side type areas	437	192,023
Totals, All areas, all years	782	361,160

*Timber types classified according to "Instructions for Making Timber Surveys in The National Forests", U. S. Forest Service, 1925.

The insects concerned in pure and mixed infestations in the infested trees were determined by sampling. The occurrence of each type of infestation was recorded on a form for that purpose. Notes were made of length of bole as well as diameter at top and bottom of each area infested by each type of infestation on each tree. All except a few of the stem analyses were of winter brood trees.

In the office the analyses were classified according to infestation types and the bark surface infested by each different infestation type was determined. These data, which are given in table 2, and supplementary descriptive notes made in the field, form the basic material used in this study.

RELATIVE IMPORTANCE OF THE SEVERAL SPECIES

It is found the importance of a given insect species depends in part on its abundance, either in pure or mixed infestations, but chiefly on its habits of attack. Some species, particularly top-killing species, may be sporadic in occurrence and not particularly abundant, yet may be important because they initiate attack. They may not be as abundant as other species following them in extension of infestation in the top-killed trees, yet are of more importance in the death of these trees.

Other species have been found to be of less importance than their abundance would indicate. This is chiefly due to the fact that their attack usually follows that of other species and is of the secondary or "fill-in" type. In practically all years and areas represented in the sample the Western pine beetle has been found to be the most abundant species.

The Turpentine Beetle

Dendroctonus valens Lec., although occasionally recorded as killing individual trees is, under forest conditions, ^{the} least important of the species concerned in infestations. In most cases it is secondary, filling in the green basal portions following attack and infestation of the remainder of the tree by other species. In some cases its attack follows injuries and initiates assault on the tree by entomological forces. However, it remains secondary in importance to the mechanical injury. In all the trees analyzed in which its attacks occurred, its role was so distinctly secondary and its occurrence of such slight importance that its presence has been ignored in tables and figures.

The Large Western Pine Engraver Beetle

Ips caryinatus (Lec.) also is of relatively minor importance although it has been found abundant on areas in the Lassen National Forest. It usually occurs alone in large trees only in relatively small patches of infested bark. More often it is associated with from one to several other species and appears to attack following infestation by them. It is of common occurrence in some stands of poor quality and in timber growing under critical environmental conditions. It often occurs as fill-in attacks on previously strip-killed trees. The species is essentially a middle and lower bole

species as indicated in figure 7.

During 1933 this species was found competing with overwintering western pine beetle brood in the Lassen National Forest. Its relatively abundant attacks appeared to be an important factor in reduction of the western pine beetle population in bark areas having this supplementary infestation. The attacking adults cleaned out and widened the galleries of the western pine beetle, destroying a considerable number of I. brevicornis eggs in the process. Eggs were laid in the usual manner and the larval brood competed with that of the western pine beetle for food. Many of the younger larval stages of that species were destroyed by the engraver beetle brood.

The Oregon Pine Engraver Beetle.

Ips oregoni (Rich.) has been found to be sporadic in occurrence. Under ordinary conditions it attacks small groups of poles in the fall of the year and infests slashings, windthrows, snowbreaks and the green tops of trees left by one type of normal western pine beetle infestation. It is confined to east side type forests in California and, under the conditions described above, is of minor importance. However, outbreaks occasionally occur naturally as well as through the artificial or accidental presence of satisfactory food material in abundance. One such natural outbreak occurred in 1932 in the Buck Creek Unit and another of minor importance occurred in the Badger area of the Modoc National Forest in 1931. Neither of these outbreaks assumed the proportions and importance of those caused by Ips confusus in west side areas.

During the 1934 season a considerable amount of activity by Ips oregoni was noted in the stem analyses of infested trees on the Lassen and Modoc forests. However, the abundance of this species appeared to be due entirely to the activity of the western pine beetle and did not represent vigorous attack on the part of the engraver beetles.

The California Five-Spined Engraver Beetle.

Ips confusus (Lec.) is very abundant and important sporadically. This species is confined to west side areas. Ordinarily it infests the same class of material as does the Oregon engraver beetle and normal infestations, although relatively unimportant, appear to be of greater importance than those of that species.

Two devastating outbreaks of this insect (1924 and 1931) have been recorded for several Sierra areas bearing ponderosa pine stands. Although, in the 1931 outbreak, this species was much less abundant than was the western pine beetle, it may have been of equal or greater importance in that it initiated attacks in the tops of many thrifty trees that otherwise might not have been killed. Though the extensive topkilling (Figures 1 & 7) of trees it also provided material that, being over seven times as susceptible as unattacked trees, was completely infested by brood of other insect species in 1932. The fact that Ips confusus is a normal part of infestations in west side type is shown by its occurrence (Table E). The sporadic nature of its

attacks is shown in the table by the three year record on Plot A. 1.7 in the Sierra Forest. Although the ecological factors underlying the los outbreak and those causing the concurrent outbreak of the western pine beetle only can be surmised, frequent recurrence of similar satisfactory conditions could make the engraver beetle of equal or greater importance than the western pine beetle. This would be in spite of the fact that the western pine beetle probably would infest the greater bark surface and would be due entirely to the method and habits of attack of the engraver beetle. There may be relationships of considerable importance hidden in the los confusus - D. brevicornis infestations of the type that occurred in west side stands in 1931.

The Mountain Pine Beetle

Field observations have indicated and recent laboratory studies have proven that the temperature requirements of Dendroctonus monticolae Hopk. brood in east and west side forests are different. The stem analyses appear to show that other ecological requirements of that species in those areas may differ considerably.

In ponderosa pine in west side areas the mountain pine beetle completely infests small trees and poles as it does in east side stands (Fig. 2). However, in the larger trees the infestation is noticeably of more frequent occurrence in the upper bole and top region (Fig. 7) than in the middle bole and basal areas of trees as is the case in east side infestations. This difference is distinct and the species, in most cases, is primary in that it either topkills or advances the infestation down the bole when attacking in west side areas.

In east side areas attacks by the mountain pine beetle, judging from the stem analyses, appear to start near the base or in the lower mid-bole region, even in small trees. Except in small trees this species appears to be entirely secondary and the infestation caused by it is of a "fill-in" type. In strip-killed or partially infested trees it is common to find late and early season attacks by the mountain pine beetle. This type of infestation is particularly noticeable in trees infested late in the season by the western pine beetle and in which the basal portion of the north side of the tree remains uninfested. The relatively great increase in importance of the mountain pine beetle in east side areas in 1933 has been considered indicative of the greater resistance to cold by larval stages. However, recent experimental results appear to indicate its resistance is not much greater than that of the western pine beetle. The slightly greater resistance may have been the deciding factor. There appears to be no other basis for an explanation of the increase.

It is suggestive of a rather free exchange of population between sugar and ponderosa pine in west side areas that the mountain pine beetle infestations in ponderosa pine are more important quantitatively and qualitatively in the SP-7 type stands than in the pure IP type forests. It also is

suggestive that the mountain pine beetle attacks start near the tops of trees in both ponderosa and sugar pine in west side areas. The marked differences in temperature requirements, habits of attack and apparent importance of this species in east and west side areas are at least interesting and may be of considerable importance.

Flathead Borers

Recent but as yet incomplete studies and rearing records indicates Melanophila californica Vandyke and not M. genilis Lec. is responsible for the greater portion of flathead infestation of ponderosa pine. Losses through attacks of this species are of such greater importance in east than in west side areas. In some areas and some seasons flathead losses have been nearly equal in amount to those caused by western pine beetle infestations.

Infestation in the west side areas is more clearly confined to top-killing and infestation of the smaller trees growing on the poorer sites (Fig. 3). However, flatheads became important following top-killing by Ips confusus in the Cascade area of the Sierra National Forest (R.S. 7) in 1931 and the 1933 record, in which flatheads entered over 26% of the infested bark surface is largely the result of attack on previously top-killed trees.

Under the environmental conditions of east side areas flathead attacks are more aggressive than in west side areas. Both large and small trees are attacked. Usually a complete infestation ensues in a single season in small trees. Larger trees may require attacks of several seasons before succumbing (Figs. 4 and 5). However, infestation by other species often takes place in such trees before a complete infestation by flathead borers occurs. The result is a large amount of bark surface infested by mixed infestations in which flathead borers may appear as an infesting species. In this type of infestation flathead borers have been considered secondary. There is abundant evidence the flathead infestation often is primary in such infestation types. Attack usually starts in the upper bole region of trees (Fig. 7) and subsequent attacks advance the infestation towards the base.

The bulk of mixed infestations that have been found are those in which the western pine beetle has attacked the lower bole. This type can, in many instances, be considered a secondary attack by the western pine beetle and an interference by that species in the more gradual but primary flathead infestation.

The Western Pine Beetle

Dendroctonus brevicornis Lbs. infested over 40% of the bark surface of the trees included in the samples in pure infestation. It entered into infestation of 67% of the entire bark surface. It is nearly three times as abundant as any other species. Pure infestations caused by that species are nearly five times as abundant as the D. brevicornis - M. californica infestation which is the type ranking second in abundance.

The western pine beetle initiates attack on many trees but there are many instances in which its attack is distinctly secondary both as to time and importance. The stem analyses, brood studies and observations on control projects have shown definitely that, in previously unattacked trees first attack is in the middle bole region and subsequent attacks occur above and below the first (Fig. 7). Often these attacks leave green tops and green bases. Green bases may fill as a result of subsequent western pine beetle attacks of the same or succeeding brood or by brood of other species. For the most part engraver beetles or flathead borers follow western pine beetles in attacking the green tops left uninfested by the original infestation.

D. brevicornis attacks occur in association with all the other species that have been discussed. In the case of Ips eximius and D. monticolae, it appears that western pine beetle attacks precede those of the other species in the majority of instances recorded. However, in west side areas the mountain pine beetle attacks may precede those of the western pine beetle. When western pine beetle broods are mixed with those of Ips gregori, Ips confusus or Melanophila californica, the western pine beetle attacks may precede as primary, follow as secondary or occur at the same time as attacks by the other species. Fig. 6 shows a group of trees in which western pine beetle attack followed that of Ips gregori in some trees and preceded attack by that species in others.

Mixed Infestations

In west side areas mixed infestations are concerned in but one tenth of the total infested bark surface. In east side areas mixed infestations are concerned in over a third of the total infested surface and the average of all samples is about one fourth.

It appears that there is considerable variation in importance and type of mixed infestations in the different areas and seasons as well as in the reasons for mixtures of the broods of two or more species. These phases of the problem will be discussed under the fourth objective of this study as listed in the introduction.

SUMMARY OF CONCLUSIONS CONCERNING THE RELATIVE IMPORTANCE OF THE SPECIES

The western pine beetle, in both east and west side areas is overwhelmingly the most abundant species. However, the analyses show infestation by that species does not stand alone but is qualitatively, quantitatively and ecologically tied closely to infestation by other species. In particular, it is probable that western pine beetle infestation, under some conditions, is of a secondary nature although apparently primary in importance.

In west side areas Ips confusus and flatheads are considered as second and third in importance. Over a longer period of record amount of loss caused by flatheads would probably be greater but in the sample the engraver beetles are more important due to their habits of attack. Their attack was primary, whereas a large portion of the flathead infestation was of a secondary nature. Because of habits of attack the mountain pine beetle is considered fourth in importance. Ips e-arginatus is of but slight importance either quantitatively or qualitatively.

In east side areas the western pine beetle infests more bark surface but it is evident flathead borer infestations, in some areas, are becoming a closer second than has been considered normal. The mountain pine beetle, because of amount of infestation and Ips oragoni, due to habits of attack can be given either third or fourth place. Ips e-arginatus, though more abundant in the sample than the top-killing species of engraver beetle is the least important of the five species in the east side areas.

COMMON AND IMPORTANT INFESTATION TYPES

Because of the many minor variations that have been found in the trees infested on the several areas that were sampled, it is an extremely difficult thing to classify all the trees into a few key infestation types. These wide variations appear to be due to area, season, or the relative degree of activity of the several species involved. However, some of the more important types of infestation may be described as follows:-

Western Pine Beetle.

Pure and complete attacks by this species are common in the east side areas (52 trees) and uncommon in west side areas (1 tree). However, the slight modifications in which attack does not extend to the 4" top diameter limit of the tree is common in both areas (74 in the east side and 35 in west side areas). In the west side areas modifications in which green bases appear bring the total trees having a pure western pine beetle infestation to 48, while in east side areas no such modifications were found and the total remains at 126 trees. The presence of green phloem in the top is probably due to a diameter limit and lack of time for secondary and supplementary infestations by other species to occur. Green basal areas appear to be due largely to the decreased active attacking population due to the ending of the active season, or to an insufficient period of time following the first attack for production of a complete infestation.

In west side areas 36 trees in the sample had pure western pine beetle infestation below top-killing caused by Ips confusus. The complete infestation occurred one or two seasons after the top-killing and, except for the increased susceptibility of topkilled trees, was otherwise unrelated to the original attack. In east side areas 8 trees had this type of attack following top-killing activities by Ips oragoni and flathead borers.

Western pine beetle-flathead borers.

This type of infestation was found to be the most important in east side areas (157 trees) and fourth in importance in west side areas (24 trees). The combination of the two species may extend from the base to the top of a tree, may exist with pure flathead infestation in the top, or with pure western pine beetle infestation in the bottom. It also may exist only in the middle bole with pure flathead in the top and pure western pine beetle in the bottom. In addition, 17 trees in west side areas had a combination of attacks by these two species filling in below previous engraver beetle topkills. In east side areas the two species infested 12 trees in combination with Ips oregoni in the top. In these trees the engraver beetles are considered secondary and flatheads primary, largely because it is evident flatheads attacked first. The reverse of this timing of attack by the two species has been found and the engraver beetles were, in those trees, considered primary.

Western pine beetle-engraver beetles.

This combination was the more important in west side areas (32 trees and 41 additional with green bases), due to the outbreak of engraver beetles that occurred in those areas during the period of record. It is believed the western pine beetle is of secondary importance in these trees, as many of them are of small size and the engraver beetles initiated attack. In east side areas Ips oregoni is the species concerned (11 trees). In 11 of these trees the engraver beetles are considered primary as they initiated attack. In four trees the western pine beetle is considered primary as partially attacked phloem in the tops was considered evidence the engraver beetle attack followed that of the primary species.

Western pine beetle-mountain pine beetle-flathead borers.

This mixture of species in which either the first or last named may be primary and the mountain pine beetle is usually of secondary importance, appears to be predominantly an east side infestation type (35 trees east side 9 trees west side areas). Broods of one or two of the species may occur in all the infested bark on a tree. Usually the three species occur together only in the base or middle bole region. Sometimes pure infestations exist in the top or bottom, flathead borers in the top and western pine beetle in the base, so that the mixture is recognized as a modification of the western pine beetle-flathead infestation type. Modifications exist in the east side areas with abandoned (old flathead) tops in 11 trees and green tops in 5 trees in which the flatheads undoubtedly are a secondary species.

Other infestation types.

Twenty-two other combinations were found in the samples. Strict notation of the species concerned shows Ips unguinatus as concerned in most of the

in east side areas. However, its occurrence cannot be considered important. That species appears as pure infestation in a portion of but one tree of one infestation type in west side areas. Pure flathead and mountain pine beetle infestations have been surprisingly unimportant in the samples. However, those species enter into most of the infestation types not yet discussed.

A few of the more important of the 22 infestation types are listed below. The total number of trees included in all these types constitutes but a minor portion of the number infested in the areas embraced by this study.

Infestation Type	Number of Trees in each Type	
	West Side	East Side
Flathead borers	2	9
Flathead borers- abandoned	18	0
Western pine beetle-mountain pine beetle	7	3
" " " " " " abandoned	6	9
Mountain " " -flathead borers	1	14
Western pine beetle-mountain pine beetle- green	0	8
Mountain pine beetle-flathead borers- abandoned	7	3

THE VALUE OF BASAL EXAMINATIONS IN INDICATING INFESTATION COMPOSITION

Most of the conceptions concerning the activity of any given species or group of species in forest insect infestations in ponderosa pine are gained through the sampling of infested trees. These samples, in ordinary cruising practice, are made in the area that can be reached from the ground, which limits them to the basal eight feet of the bole area. It is essential that the value or lack of value of the information obtained by this method be determined. Except for observations concerned with the intangible impressions gained from the general appearance of an infestation in a given area, or the costly and little used stem analysis method, there is no other method available for determining the relative amount of activity of the infesting species.

Accordingly the stem analyses have been examined with the object of determining the value of basal examinations in indicating the composition of infestation in individual trees or types of infestations.

If *P. valens* and *Ips emarginatus* (with the exception of 1 tree having pure infestation by that species in the stem) are ignored in determining the infestation type combinations, it is found (a) 11 combinations would have no insects in the sample; (b) 32 combinations would have one species in the sample; (c) 14 would have two species and (d) 2 would have three species. Of these 72% in west side areas would have one species and 67% in east side areas would be cruised with cause of death attributed to one species. In our sample, no types in the east side would be cruised without finding insect brood and no west side types would be cruised with a mixed infestation involving two species. However, individual trees in those types do occur in the areas in which they did not appear in the sample.

Out of a total of 60 combinations, 33 were found in west side areas. Twenty-eight of these contained less than 10 trees each, constituted 24.9% of the total number of trees and could be considered either minor variations of major types or relatively unimportant combinations. Five contained more than 10 trees but less than 20. They can be considered common types and constituted 22% of the number of trees in the west side samples. Five other combinations were abundant, contained 83.6% of the trees and can be considered predominant types.

Of the 60 combinations, 33 were found in east side areas. Twenty-seven of these contained less than 10 trees or 29.1% of the total number. Two contained more than 10 but less than 20 and can be considered common types. These contained but 6.6% of the total number of trees. Four combinations were predominant and contained 64.3% of the total number of trees.

Of the predominant combinations, 2 were neither common nor predominant in west side areas, 3 were neither common nor predominant in east side areas and two were predominant in both areas. These predominant combinations are as follows:

Sample: Complete Infestation from area : bottom to top				Predominant in
1-	Green	Green-DB-	DB-Ips- Ips	West side area
2-	DB	DB		East side area
3-	DB	DB-Green top		Both areas
4-	DB	DB- Abandoned (Chiefly Ips)		West side area
5-	DB	DB- DB, FH- FH		Both areas
6-	DB	DB- DB, Ips- Ips		West side area
7-	DB, FH	DB, FH- FH		East side area

Of these combinations, the pairs 1 and 6, 2 and 3, 5 and 7 are essentially slight modifications of the same types of attack.

In the first combination sampling would not give the cause of death. If the western pine beetle infestation extended far enough down the bole evidences of attack might be seen. In the sixth combination, cause of death would be attributed to the western pine beetle, as it might be ascertained for trees in the first group. However, primary cause of death would not be determined by anything but intuition for, in the type of attack represented by these two groups, stem analyses have shown the engraver beetles usually attacked first and were primary, the western pine beetle being the secondary species.

In the second and third combinations the infestation is essentially the same. These combinations were common following the peak losses of 1931 and 1932 in west side areas and in 1932 in east side areas. Usually they are concerned in the spectacular infestations and appear to be the result of momentum or force of heavy populations. The correct cause of death would be determined by basal examination and the western pine beetle would be primary. However, as is shown by the other combinations listed above, and as is true of many of the other common or minor infestation combination types, the

presence of the western pine beetle alone in the base is not peculiar to trees having primary and pure infestations by that species. In the sample but about one-third of the trees that would be marked as having a pure western pine beetle infestation would actually contain one.

In the fourth combination there may be some question as to whether the topkilling or the western pine beetle infestation is primary. However, an uncompleted analysis of topkilling by *Ips* in the Sierra areas has shown top-killed trees are 7.9 times as susceptible in the season following top-killing as those not having that injury. With this in mind there is little doubt a basal examination would not indicate the primary cause of death, although it would indicate the species infesting the greater bark area.

In the seventh combination the presence of flathead broods in the base merely represents a greater extension of flathead activity in the tree before the supplementary and secondary infestation by the western pine beetle took place. In the fifth group the primary cause of death could not be determined by basal examination. Intuition or uncommonly keen observation might detect the flathead activity in the top of the tree but determination of that species as the primary insect would have an insufficient basis. In the seventh group flatheads could be detected and should be considered primary. However, without the knowledge of habits of attack and the primary nature of attacks by that species that has been a result of this study, the flatheads at the most would have been considered a co-primary species.

Analyzing the stem analysis data we find basal cruises would determine the primary cause of death in the predominant infestation types correctly in but 36 out of every 100 trees. Even with our present basis of stem analysis data, it is impossible to correctly determine the primary cause of death in all cases. This is true particularly of those infestation combinations in which two or more species infest the greater portion of the bole. However, it appears probable that basal examinations reveal the primary species in but about one tree in every four.

A few general conclusions can be drawn from the stem analysis data. In west side areas, it so happens the amount of western pine beetle infestation indicated by basal examinations is about the same as the actual amount determined by stem analysis. This cannot be said of east side area infestation samples. When pure or mixed flathead infestations are found in the base of a tree, it seems certain, on the basis of our sample, that the species will be found throughout the infested bark area. Small trees (less than 500 b.m.) containing mountain pine beetle broods in the basal area usually contain brood of that species in most of the infested bark area. When *Ips* (not *erat. inatus*) broods are found in the base, it is indication that species is a major species in the infestation of that tree.

THE CAUSES OF VARIATION IN COMPOSITION OF INFESTATIONS

Variation in the composition of forest insect infestations in the areas sampled and over the period of record includes (1) variation in

the amount of infestation caused by a given species or combination of species; (2) variation in the portion of tree attacked by a given species or infestation type; (3) variation in quality of infestation from year to year in a given area, or (4) variation in quality of infestation in different areas. It is believed the basic information secured for this study, in connection with supplementary observations and study of other data that these variations are due primarily (a) to the variation in critical environmental conditions from year to year; (b) to the variation in the relative amount of activity by the several species; (c) to the factor of time as it concerns seasonal activity, timing of attacks in mixed brood trees and rapidity of development of the several species. These last two factors are, of course, closely associated with physical environmental factors.

Variation in environmental conditions.

It is not considered the record long enough, the identity of the critical environmental factors well enough established, the existing measurements of their intensity accurate enough, the present knowledge of their effects on the insect species well enough known, or the problem simple enough to warrant an analysis of the relationships of environmental factors to the yearly variations.

There does, however, appear to be some basis for considering some environmental factors in relation to the geographical differences in infestation composition.

It has already been pointed out that, in west side areas, the mountain pine beetle enters into a larger proportion of the infestation in the M-PP type stands. This is suggestive of a free interchange of population between sugar and ponderosa pine. However, it may also be due to the more satisfactory conditions for that species in the colder and moister areas in which sugar pine occurs as an important part of the stand. Similarly the mountain pine beetle plays a more important role and is more abundant in the higher and moister areas of the Lassen Forest in east side type stands. Flathead borers in west side areas are more active in the infestation at the lower elevations and in the pure ponderosa pine type. They also are more important in the lower and dryer areas in the Modoc and Lassen Forests.

Marked differences in infestation composition are noted between the east side areas, which lie in the 0-20 inch precipitation belts and the west side areas that lie in the 20-40 inch precipitation belts. These differences take the form of a greater amount and importance of mixed infestations, increased importance of flathead borers, decreased importance of engraver beetles, exclusive of Ips emarginatus and western pine beetle broods, in general, entering into a greater proportion of the infested bark surface in the dryer areas. Other data, not connected with infestation composition studies, appear to point to moisture supply as at least partially responsible for these differences.

Variety in activity of species.

In west side areas, more particularly on the Cascadel plot (R.S.7) in the Sierra National Forest on which a 3 year record has been secured, the variation in relative importance of one species is marked. Its activities in one year appear to have affected the activities of two other species in the two seasons following the year in which the outbreak occurred.

Ips confusus caused a large amount of top-killing in 1931 and was active. In the two years following that season, its activity was reduced to a relatively low level, probably due to the natural course of the infestation cycle. Western pine beetle activity increased in the year following the engraver beetle outbreak, and that species assumed a place of greater importance in the infestation. This increase appears to have been due largely to infestations of previously top-killed trees. A decrease was recorded in the second year after the Ips outbreak. This decrease coincided with similar natural decreases that occurred throughout similar west side areas. In contrast to the decrease in engraver beetle activity, flathead borers showed a marked increase in relative importance in the second year following the Ips outbreak. This, from stem analyses, has been found to be the direct result of the fact that a large amount of top-killed material was available and that the western pine beetle population was relatively inactive. Flathead broods were responsible for the death of many of the previously top-killed trees in 1933. The increase in the relative abundance of abandoned bark surface that was found in the 1932 and 1933 stem analyses, also is the result of the 1931 engraver beetle outbreak.

In the east side areas it is possible that the decreased population of the western-pine beetle available for infestation in the 1933 season following reduction due to low temperatures is responsible for the increase in the relative importance of mountain pine beetle and flathead borer broods. However, these variations appear to be more closely related to a slightly greater resistance to low temperatures than to the activity of any given species.

The time factor.

Study of the stem analysis records show time is an important factor in determining the composition of infestations. The time element, as it concerns changes in composition with the passage of years, of course plays an important role in that changes in infestation cycles of individual or aggressive species of primary insects are related to it.

During a single season the timing of emergence of the several species of insects and their periods of flight and attack appears to modify the composition of infestations considerably. It is impossible to discuss all the details that are made apparent by the stem analysis records, but the following two examples are typical. At a different time of the year, these types could not have occurred or would have been different.

In west side areas the infestation types in which the western pine beetle and Ips confusus were combined, were common in 1931. Many of these trees had been abandoned by Ips in the top; had well developed Ips broods below; young Ips broods and DB brood below that and pure DB brood towards the base. The time element in this case functioned, as follows, to produce that type of infestation. The first attack was by Ips in the top and brood developed. A second attack infested a band below the original top infestation. About that time DB attacked the midbole and subsequent attacks by that species spread towards top and base. Before that species was able to completely infest the tree to the Ips attack above, the original Ips brood emerged as new adults and attacked in conjunction with DB below the second Ips infestation. It is not assumed that the successive Ips attacks were the result of emergence of parent adults or brood from the same tree, but the evidence is that the time element of emergence and attack made that possible. It also is evident that, particularly late in the season, a supplementary and secondary attack by flathead borers, mountain pine beetle, turpentine beetle, or Ips emarginatus may occur in an uninfested or relatively lightly infested phloem area near the base.

In east side areas the flathead-western pine beetle type of infestation is common. There is abundant evidence infestation in many of these trees starts with flathead attack in the top. Sometimes two or more years pass, with successive attacks by flathead broods before complications begin. The tree becomes weakened and finally the western pine beetle attacks below the newest flathead attack. If the flight season for flatheads is at hand the two species may attack a portion of the bole together, or the western pine beetle may fill in areas recently attacked by flatheads. There is some evidence supplied by observations made in connection with brood studies that flatheads do not attack following a normal infestation of the phloem by western pine beetle broods. In the midbole and base, particularly when the western pine beetle attacks are not heavy, either the mountain pine beetle or Ips emarginatus may enter into the infestation.

The examples given above are considered sufficient to illustrate the many complications in infestation composition that are the result of the time factor in its relation to the species concerned in infestation of a given tree.

CONCLUSIONS

The information on which this paper is based has shown the following:

1. The western pine beetle is the most abundant insect concerned in forest insect infestations of ponderosa pine in California. Its primary importance may be overestimated.
2. Flathead borers are second in abundance, appear to have been increasing in importance in recent years and, due to habits of attack in east side areas, may be the primary insect in many of the trees customarily considered to have been killed by the western pine beetle.

3. Ips confusus, in west side areas, is sporadic in occurrence, but in the sample is second in importance. Although flatheads are slightly more abundant, they are given third place due to the primary nature of the Ips attacks.
4. The mountain pine beetle is considered fourth in west side areas and Ips erarginatus is a poor fifth. In east side areas the mountain pine beetle is considered third, due to its abundance; Ips oregoni is fourth due to habits of attack; and Ips erarginatus is fifth in spite of its greater abundance.
5. There is a great variation in the types of infestation. Besides 22 different combinations which, taken together, are of minor importance, 38 other combinations can be grouped into the four important primary types of (1) pure DB attacks, (2) DB-PS in combination, (3) DB-Ips in combination and (4) DB-PL-PS which, in east side areas, is but a modification of the second group.
6. With the exception of flatheads in trees of any size, and mountain pine beetle or top-killing engraver beetle species in small trees, the presence of the brood of a given species in the base of a tree is little indication that the species is concerned in the major portion of the infestation of an individual tree. In west side areas the presence of DB in the base was indication that it entered into the major portion of the infested bark area in our sample. However, in east side areas that was not found to be true.
7. It seems that variation in forest type - which may be but an expression of variation in physical environmental factors - is responsible for variations in the relative importance of the mountain pine beetle and flathead borers. The precipitation deficiencies seem to be linked with the large amount of mixed infestation found in east side areas.
8. The activity of Ips confusus in 1931 influenced the composition of infestation in west side areas considerably. The relative importance of western pine beetle and flathead borers in the two years following the attack appears to have been linked to the Ips outbreak.

The data supplied by the stem analyses makes it evident that corrections should be made in our assumptions concerning infestations and in our conception of the relative importance of the roles played by the various insect species. The conclusions resulting from this study are as follows:

1. Cruise results- interpreted strictly on the evidence of basal examinations - are expressions only of the sum total of forest insect activity. It may be, when totalled for an area, an expression of abundance of a given species is secured, but they do not appear to be an accurate expression of importance of a given species. Supplementary observations by trained and keen

observers appear to be a more reliable index to the importance of individual species providing the relative importance of different species or types of attack are correctly understood.

2. The fact is established that abundance and importance of a given species have different bases of measurement. The most abundant species may not be the primary insect in a tree or area. The question is raised as to the overwhelming importance of the western pine beetle in considering forest insect infestations in California as a whole. It is recognized that species is the primary insect in many trees. The data show, however, that so-called secondary species, particularly Ips confusus and Melanophila californica say, in infestations over relatively large areas, be the primary species and cause the death of the majority of infested trees. These facts and indications suggest the necessity for a critical revision of our present conceptions.
3. Forest insect infestations are ecological complexes. As a whole no one species stands alone. Each affects and is affected by the activities of associated species. This applies to most individual trees (but 20% of the trees had pure infestations) and particularly to infestations where area is concerned. This fact must be considered carefully in control recommendations as to technique of treatment and, more particularly, is a factor of considerable importance in investigative work.

RECOMMENDATIONS

It is considered the basis of 782 stem analyses is sufficient for the conclusions that have been drawn. However, it seems advisable to secure records of the complete infestations on given areas and over a series of years.

It is considered advisable also to probe further into the relations of the various species in given trees or in given areas. Present plans call for employment of a survey crew in connection with work on the Black's Mountain Experimental Forest and the salvage control operations in the Lassen and Shasta National Forests. This crew can secure a considerable amount of information in connection with these projects, although it would be more satisfactory to assign men definitely to this project.

The ecology of the several species of forest insects, particularly in their relationships to each other, is practically a virgin field. Inasmuch as the possibilities of actual forest insect control appear more likely through modification of environmental conditions, it is necessary we understand the ecological requirements of the interdependent entomological factors.

As the results of this study have made it necessary to question the premises on which some of our investigations have been based, it appears desirable to sponsor an inquiry into our present theories and assumptions.

TABLE II
COMPOSITION OF INFESTATIONS
BASED ON STEM ANALYSIS

		PERCENT OF TOTAL BARK SURFACE INFESTED BY															old					total bark surface entered by				
Forest	Plot	Year	Green	DB	DM	FH	I	I.em	DB-DM	DB-FH	DB-I	DB-I.em	DM-FH	FH-I	DB-DM-FH	DB-FH-I	Infestations	DB	DM	FH	I	I.em				
Sierra	R.S. 7	1931	11.3	54.1	0.1	4.8	16.3			4.1	4.6			0.2	3.6		0.2	0.7	63.0	0.3	12.7	24.9				
	"	1932	7.6	70.6	2.3	5.6				1.4	0.3		1.4				10.8	72.3	3.7	8.4	0.3					
	"	1933	1.1	50.8	1.6	16.7	3.0			7.9			2.0				16.9	58.7	3.6	26.6	3.0					
	8	1931	18.5	57.8		5.9	3.0			8.9			1.2		0.8		3.9	66.7	1.2	16.8	3.8					
	"	9	1931	12.2	73.4		5.8	1.0	0.7		3.1					1.4	2.4	77.9	1.4	10.3	1.0					
	"	10	1933		68.0	21.8		2.9									7.3	68.0	21.8		2.9					
	"	12	1932	13.2	75.6	1.1	0.5	2.6		1.4		0.4					5.2	77.4	25.0	0.5	3.0					
	"	12	1933	4.5	70.4	5.3	1.6	2.4		10.0						3.9	1.9	84.3	19.2	5.5	2.4					
Stanislaus	"	14	1932	19.7	47.8	5.8	2.2	2.8		7.8	0.6	2.1	2.1	0.6	0.7		4.4	59.7	16.3	6.8	5.6	2.1				
	"	14	1933	12.0	30.9	7.9	3.1	0.4		22.7		1.4		1.2			20.4	55.0	31.8	4.3	1.8					
Modoc	Badger	1931	1.2	26.3		16.0				0.3	49.3			0.8		0.5	1.8	0.2	3.6	77.9	2.9	68.6	0.7			
	"	1932	7.5	74.4		4.3				1.6	6.0						2.8		3.4	84.8	4.4	15.5				
	"	1933	6.5	31.3	3.7	22.0				7.5	19.2			3.3			6.2		0.3	64.0	20.7	50.7				
	R.S. 11	1932	6.0	83.7		1.5	0.6	0.2		1.5	0.2	0.1		2.9	11.0		0.6	1.2		0.4	89.6	3.8	4.6	1.3	3.1	
Lassen	Las. 6	1933	7.2			15.8				20.0	23.1			16.5			17.4			60.5	53.9	72.8				
	"	2	1934	4.6	41.1	1.8	4.5	0.6	0.5	3.7	16.4		9.5	3.4			5.1		8.8	75.8	14.0	29.4	0.6	10.0		
	"	3	1934	5.3	51.5	1.6	2.9	0.8		11.8	13.0		1.4	4.9		0.1	4.1		2.6	81.8	22.4	25.0	0.9	1.5		
WEIGHTED AVERAGES																										
West Side Areas			10.11	59.55	2.04	5.14	6.81	0.08		2.13	3.36	1.77		0.11	0.57	0.10	1.24	0.39	0.06	6.03	57.29	5.23	11.28	10.01	0.11	
East "			4.41	44.99	0.95	9.84	0.30	0.09		4.51	23.51	0.01		1.90	2.55	0.03	0.25	3.58	0.06	3.22	78.54	11.60	39.85	0.63	2.00	
All Areas			7.08	51.81	1.46	7.77	3.36	0.06		3.40	14.07	0.84		1.06	1.63	0.05	0.72	2.09	0.06	4.54	73.27	8.62	26.47	5.03	1.12	

FIG. 7

DISTRIBUTION OF ATTACKS
IN
INFESTED PONDEROSA PINE

Density of stippling indicates frequency of occurrence in the samples. Heavy shading in 1, 2, 4, and 6 indicates location of first attacks.

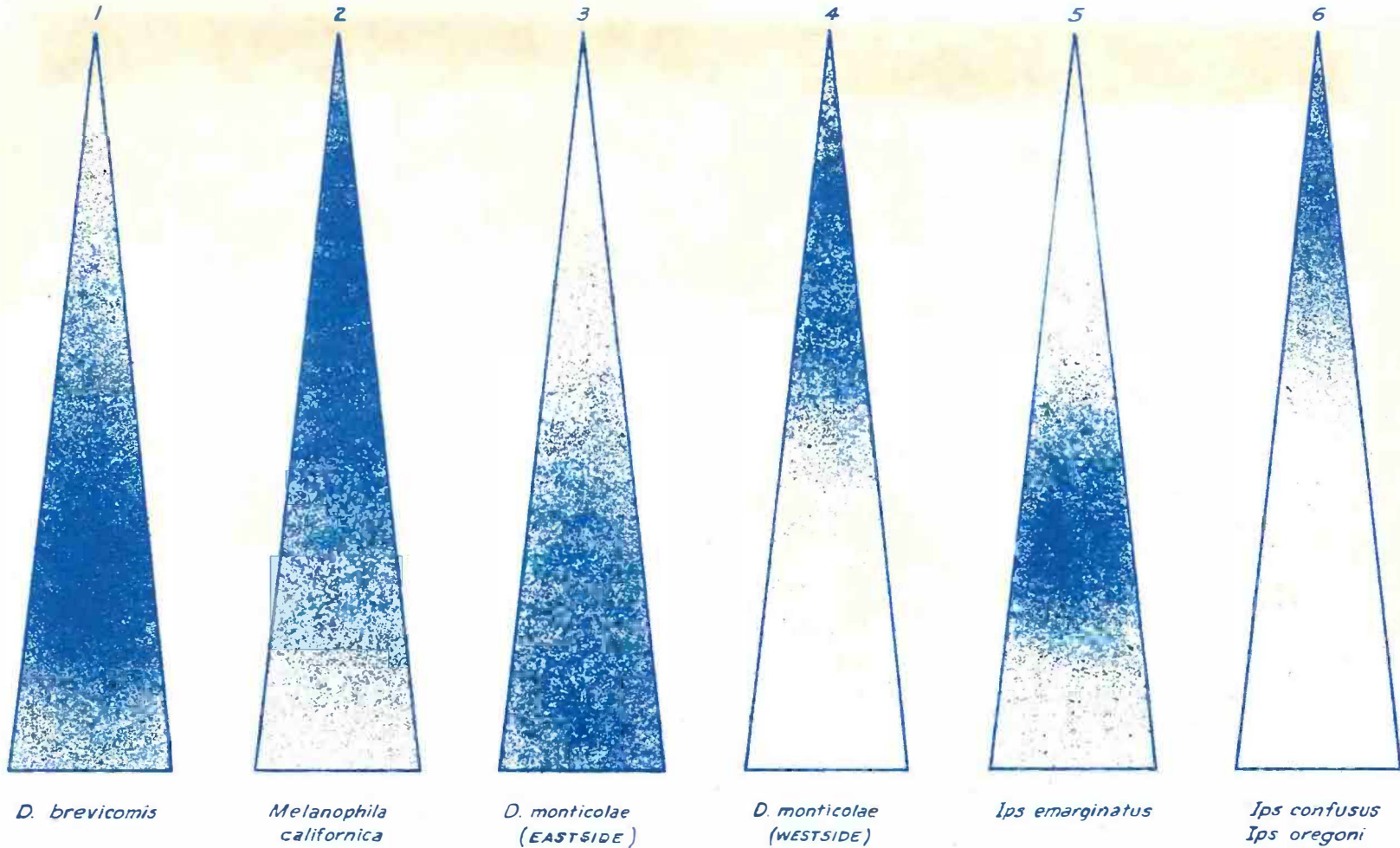


Fig. 1

Sierra National Forest

June 11, 1933

Top-killed ponderosa pine showing typical attacks by Ips confusus. The trees shown were uninfested below the point where foliage had not faded.

Photo #7403

K. A. Salman

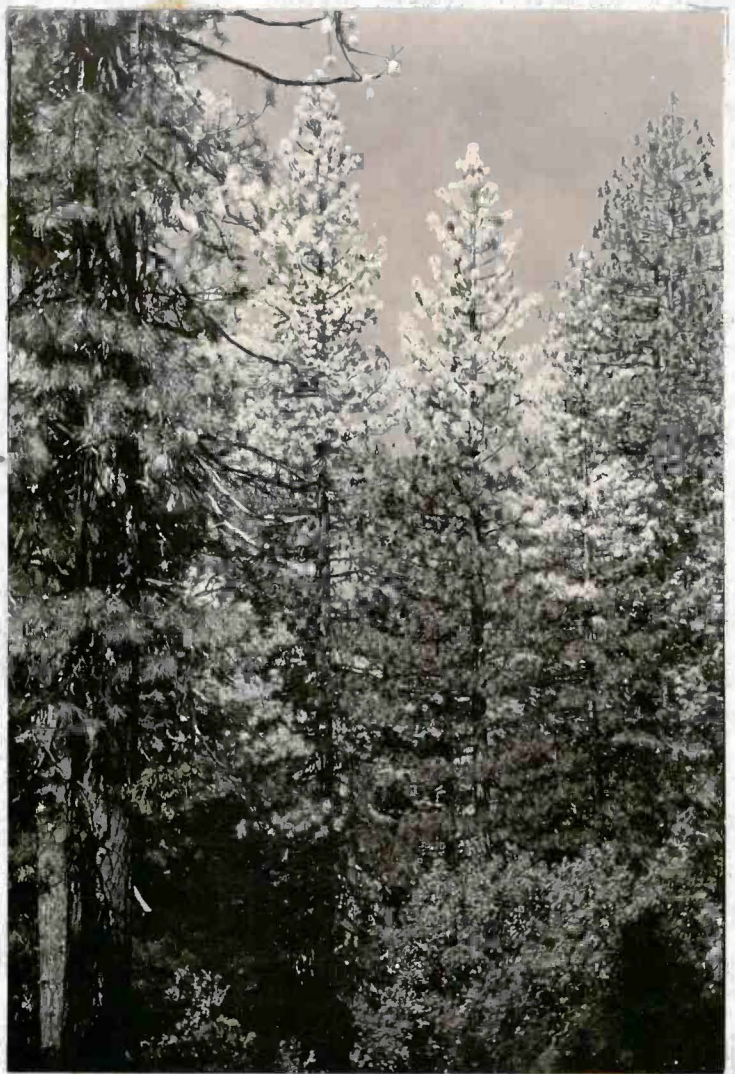


Fig. 2

Last Chance
Plumas National Forest

June 11, 1933

Ponderosa pine poles and reproduction killed by attacks by Dendroctonus monticolae. This is a primary type of attack and occurs normally to individual poles and suppressed trees in mature stands.

Photo #7406

K. A. Salman





Fig. 3. Folsom Ranger Station, Stanislaus National Forest, August 3, 1932
 ponderosa pine reproduction in the foreground was attacked by flathead
 borers. This type of attack occurs in the larger reproduction, poles
 and young trees growing on the poorer sites. Topkilled trees in the
 background resulted from attacks by engraver beetles. No. 7565, E.A. Salzen.

Fig. 4.

Hackamore, Modoc
 National Forest.
 April 18, 1934.

Relatively thrifty
 mature tree showing
 successive attacks
 by flathead borers.
 First attack occurred
 in the top, which
 shows no foliage and
 successive broods
 attacked base and the
 lower crown foliage
 was green.

Photo 77484
 E. A. Salzen

Fig. 5

Hackamora
Modoc National Forest
March 20, 1935

Same tree as shown in
Fig. 4. Most of the foliage
shown red in that figure
has fallen and all foliage
is sorrel or faded. Examination
showed flathead broods
in the larval stages near the
base.

No. 8437, K. A. Salvan



Fig. 6

Buck Creek
Modoc National Forest
October 6, 1932.

Group of ponderosa pine which
on stem analyses revealed
preliminary attack in tops
by Ips oregoni, followed by
supplementary infestations
in the bole regions by Dendroctonus brevicornis, and
primary attacks in the bole
by D. brevicornis, followed
by secondary attacks by engraver beetle in the tops.

Photo #7493A- K.A. Salvan

FIG. 7

DISTRIBUTION OF ATTACKS
IN
INFESTED PONDEROSA PINE

Density of stippling indicates frequency of occurrence in the samples. Heavy shading in 1, 2, 4, and 6 indicates location of first attacks.

